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CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS[1]

I. Scleropteris, gen. nov., Mesoxylon and Amyelon

HENRY N. ANDREWS

Instructor, Henry Shaw School of Botany of Washington University

The occurrence in America of the petrifactions known as coal-balls has been known for many years and in itself needs no review. It is, however, still rather generally accepted that American coal-balls are by no means the equal of the renowned English specimens that have yielded such a wealth of information concerning the flora of Carboniferous times. Much of the American material is highly pyritized, and although pyrite does not necessarily render the petrifactions worthless it is not the most desirable preserving mineral. Pyritized material from the English mines is by no means unknown, while many of the American specimens are quite free from pyrite or contain but insignificant quantities and the plants contained in the coal-balls often exist in an exquisitely fine state of preservation.

It has been my privilege to study rather carefully most of the great English collections of petrified Carboniferous plants, and from a comparison of those with some hundreds of Illinois specimens that have recently come into my laboratory there is no doubt that the better ones are equally as well preserved as the English. The commonly encountered "open pit" method of mining in our central states is making huge quantities of material available, and much may be expected of the ensuing studies on American paleobotany during the coming years. It must be remembered, moreover,

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that the outstanding English collections and the slides dispensed by professional petrologists represent the choice selections of nearly a century of labor, while almost nothing has been done with American coal-balls until a very few years ago. It is safe to assert that when our own flora is better known it will not suffer by comparison.

Although a considerable number of species have already been reported from the petrifactions of the midwestern states (Darrah, '41), few comprehensive studies have been undertaken. It is planned to present here, and in the following parts of this series, descriptions of the plants composing the coal-ball flora, chiefly of southern Illinois. As it is not possible to present the results of such a study in phylogenetic order without undue delay, they will appear as adequate material of the genera is collected and studied.

All of the specimens on which the present paper is based were collected by the author and his students from the open-pit Pyramid Mine of the Binkley Coal Co., located about three miles south of Pinckneyville, Perry County, Illinois. I wish to express my appreciation for the very generous assistance and cooperation extended to me during many visits by officials and employees of that mine.

The petrifactions are abundant, although, as might be expected, they are by no means uniformly distributed through the coal. One may chance upon a "nest" of half a ton or more or wander along the seam for a mile without encountering any. The better coal-balls are usually found near the top of the seam, sometimes a foot or so below the surface, but more often than not in sheet-like aggregations, their tops flush with the surface of the coal. They are easily detected when the latter is exposed and slightly weathered. The mineral content of these more or less unit aggregations seems to be quite constant, and in many cases they are very nearly free of pyrite. Thus it is a rule that when one or two good specimens are picked up, dozens of others are near at hand.

The better coal-balls lend themselves readily to the preparation of satisfactory nitrocellulose peels, although it has been found necessary in some instances to use them in conjunction with ground sections.

Arborescent Lycopod stem remains constitute the dominant floral feature of our collections. Associated with them are *Lepidophyllum, Stigmaria* and *Lepidocarpon.* A consideration of the stems and leaves will be presented at a later date, while a description of a remarkably well-preserved gametophyte and the microsporangiate cones of *Lepidocarpon* constitutes the second contribution of this series (see p. 19). Stems and roots of *Sphenophyllum* are well represented and fructifications probably referable to *Scolecopteris* occur in many specimens. *Heterangium* is also present. Stems and roots of *Mesoxylon* are common, and these, together with a new genus of coenopterid ferns, will be considered in the following pages.

Scleropteris illinoiensis Andrews, gen. et sp. nov.

General Anatomy and Procedure.—

Our knowledge of this pteridophyte is derived from a small portion of a branched stem which, although fragmentary, is excellently preserved. Since but one specimen has been encountered in some hundreds of coal-balls, it seems desirable to describe it without further delay. As will be pointed out in the following pages, *Scleropteris* resembles in some respects *Botrychioxylon* and *Zygopteris* but certain highly distinctive features of the cortex, as well as the tracheidal pitting, set it apart from these two genera (or one, as Sahni ('32) has shown may be the case).

The specimen was about 6 cm. long and branched twice. Prior to the first division, an equal dichotomy, the stem measured 1.3 cm. in diameter. Shortly after the dichotomy of the stele the stem became somewhat flattened, measuring 1 × 2 cm., and the two resultant branches each measured 1 cm. in diameter. These figures are necessarily approximate due to some slight crushing and distortion.

The most distinctive feature of the stem lies in the sclerotic nests scattered through the broad cortex. The stele consists of a mixed primary body surrounded by more or less radially arranged tracheids presumably of secondary origin. Adventitious roots are numerous.

The specimen was cut into three slices perpendicular to the long axis of the stem. The central section was used for a series of longitudinal peel preparations, the other two for transverse sections. Unfortunately, the initial saw cut passed directly through the point of dichotomy of the stele.

Preparations made by the nitrocellulose peel technique proved very satisfactory. In fact, in this particular case they were superior both for study and photographic purposes to ground sections. It was found that by photographing the peels unmounted, rough side down, against a black background, excessive reflection was reduced and much finer detail was obtained than when the peels were mounted in balsam.

The Stele.—

Figure 2 of pl. 1 represents a transverse section of the entire stem prior to dichotomy, while fig. 1 shows it shortly above the division of the stele. It may be noted that the dichotomy is equal, both branches (pl. 1, fig. 1, st_1, st_2) being approximately the same size. The stele itself, taken from a point about 1 mm. above the section represented in fig. 2, is shown more highly enlarged in fig. 3. At this point, which is immediately prior to dichotomy, it is oval-shaped but is otherwise nearly circular in cross-section (pl. 3, fig. 11). There the stele measures 2 mm. × 3.5 mm., while after division the resultant branches are approximately 1.3 mm. in diameter.

The central part of the stele is mixed, being composed of small tracheids scattered through the parenchyma cells. The latter may be isodiametric but for the most part are vertically elongated, being 2–4 times as long as broad. It is not possible to distinguish definitely protoxylem elements in transverse section. In median longitudinal sections, however, small scalariform tracheids may be observed near the periphery of this primary mass (pl. 2, fig. 7, *px*). It would thus seem that the primary wood was mostly centripetal, as is probably the case in *Botrychioxylon paradoxum,* but this point is not without an element of doubt in both species.

Around the mixed primary xylem there is a zone of larger tracheids, for the most part radially arranged and presumably secondary in origin. These are uniformly pitted on both radial and tangential walls. Some of the small tracheids located near the inner margin are scalariform but all of the larger ones possess multiseriate bordered pits although they may be slightly elongated horizontally (pl. 2, fig. 7). With reference to the pitting of *B. paradoxum,* Scott ('12) writes: "The large tracheids of the secondary wood have scalariform markings, the bars being often short, so that there are two or three series on the same wall." [p. 376]. His fig. 21, pl. 41, bears out this description. The pits are much less closely compacted in *Scleropteris,* and although there are transitions between scalariform and nearly circular bordered pits the latter are distinctly predominant.

Since no tangential sections of *B. paradoxum* were prepared, the presence of wood rays was left in question. Scott writes: "It is doubtful whether true medullary rays are present; if so they must be very few in number. Transverse sections afford no decisive proof of their existence." [p. 375]. It is likewise difficult to discern rays with certainty in the cross-sections of *Scleropteris* but serial longitudinal sections reveal their presence. A tangential section from near the outer margin of the secondary wood (pl. 3, fig. 12) shows uniseriate rays of great height.

The secondary wood is not extensive, varying from 5 to 9 cells wide. The cells are, for the most part, radially arranged and occasional evidence of cambial activity at the periphery leaves little doubt as to its true secondary origin.[1]

Although the tissues immediately outside the xylem are not as well preserved, in certain sections there may be observed a narrow phloem, a pericycle two cells wide and what appears to be an endodermis the cells of which are filled with a very dark substance. The endodermis is, however, not readily distinguishable in most sections, as might be expected where an appreciable amount of secondary growth has taken place.

The Cortex.—

The most prominent feature of the stem lies in the abundant sclerotic nests scattered through the cortex (figs. 1, 5, 6 of pls. 1–2). Although rather irregularly shaped they appear more or less isodiametric in cross-section and slightly elongated longitudinally (figs. 5, 6). The sclereids composing the nests are very thick-walled, in some the lumen being almost lacking. Like the nests as a whole, they are slightly elongated longitudinally.

The outer parenchymatous cortical cells contain an abundance of branching fungal filaments. Although they may compose the mycelium of a decay organism, their aggregation within the cells suggests a mycorrhizal relationship.[2]

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[1] It is evident from recent anatomical studies that the distinction between primary and secondary vascular tissues is not as sharp a one as was once supposed, and it is possible that these radially arranged tracheids have had their origin from a multiple ("primitive") cambial layer rather than a single row of meristematic cells.

[2] *Mycorrhizae and the origin of roots:* The presence of mycelium in the tissues of fossil plants is not uncommon, and it occurred to me some few years ago that there might be a deeper lying significance to this association than most authors realized. The idea, and I do not claim absolute priority although I know of no published formulation of it, seems worthy of some thought. Briefly stated, it seems possible that mycorrhizae or a mycorrhizal-like association were a deciding factor in the establishment of the higher land plants and that root hairs and rhizoids are the result of later specialization in the higher vascular plants and the lower vascular plants and bryophytes respectively.

It is supposed that mycorrhizal associations existed prior to the evolution of the normal absorbing organs of these plants and that as the aquatic ancestors migrated landward the mycorrhizae made possible this new habitat; and as these newly arrived land plants

The cells of the outermost cortical layers and epidermis are arranged in peculiar mounds which seem to represent the basal portions of emergences (pl. 1, fig. 4). Whatever was the nature of such emergences is not known. Most of them terminate in a flat top as shown in fig. 4. That they do represent the basal part of a superficial appendage seems certain as their remnants are present in some of the sections and none show evidence of having possessed vascular tissue.

Petioles are lacking in the single available specimen. It was thought at first that the small branch shown at the right of fig. 5 might be a petiole but the serial longitudinal peels reveal no positive evidence of a leaf gap at its junction with the main stem stele. The specimen is, then, either a fragment of a plant bearing rather widely separated nodes or it is one in which there is no distinct segregation of the shoot system into stems and leaves as they typically occur in more recent groups.

Roots.—

Adventitious roots are numerous throughout the specimen. Three may be seen in various stages of departure from the stele in pl. 1, fig. 3. The passage of the root stele through the cortex is irregular but in most cases it appears to be upward at an angle of about 30° with the stem stele. It is not possible to determine for certain the number of protoxylems. There seems to have been some secondary xylem, as well as cork cambial activity, and the cortex is comparatively broad.

Diagnosis.—

A dichotomously branching stem 1–1.3 cm. in diameter; stele consisting of a central mixed primary region, probably centripetal in development, surrounded by a zone of radially arranged tracheids

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became better adapted to their new habitat they developed rhizoids or root hairs and roots which gradually replaced the fungus. There are a number of points that lend support to such a hypothesis. Roots are lacking in the earliest land plants but rhizoids are present and in certain cases fungal associations that may be mycorrhizae; roots are not strongly developed in the higher vascular cryptogams as a whole; in certain seed plants it is well known that germination of the seeds and early growth of the young seedling is difficult or impossible without mycorrhizae.

The possibility is, of course, clearly recognized that the rhizoid-like structures present in the algae may have given rise directly, in all instances, to the corresponding structures in early land plants. This concept of the part that mycorrhizae may have played is presented for what it may be worth.

bearing multiseriate bordered pits on radial and tangential walls; prominent sclerotic nests scattered through cortex.

Affinities of Scleropteris.—

As far as stelar structure is concerned, the affinities of this genus appear to lie with the zygopterid ferns, with which it agrees in the division of the stele into a central mixed pith and a peripheral region of comparatively large tracheids. In both *Ankyropteris* and *Zygopteris* a weak development of secondary wood has been reported. Compared to these two, the tracheids of *Scleropteris* seem to be much more regularly arranged and more distinctly secondary. Of the described species of *Ankyropteris* the closest comparison is with *A. corrugata* (Holden, '30) but in that species the tracheids are typically scalariform, quite in contrast to the multiseriate and nearly circular pits of *Scleropteris.* The closely compacted leaf bases of *Zygopteris* and the branching of the stem in *Scleropteris* present contrasting characters which sharply separate these two genera.

The cortical sclerotic nests of *Scleropteris* constitute the most distinctive feature of the fossil and set it apart from any other fern referred to the Coenopteridineae (classification of Hirmer, '27). These structures are of interest not only for their diagnostic value but because they suggest these possible affinities with the pteridosperms. First, one of the most prominent features of that group is the dictyoxylon cortex so strikingly displayed in *Lyginopteris.* It seems evident that this tissue must have had its origin in a less highly organized arrangement of parenchymatous and sclerotic or fibrous cells, and the scattered, slightly vertically elongate nests of *Scleropteris* may represent a step in that direction. Second, the radial arrangement of the tracheids indicating weak cambial activity points in a gymnospermous direction.

Mesoxylon.—

Judging from the frequency of occurrence of Cordaitean stems and roots in the Pyramid Mine petrifactions, this group was well represented in the Carboniferous Lycopod forests of southern Illinois. The stem remains described below are referable to *Mesoxylon,* and although in themselves they present only such features as are already known in the five English species, it has been possible to demonstrate that roots of the *Amyelon* type, long considered to be of Cordaitean affinities on the basis of association, actually occur in organic connection with *Mesoxylon.*

The stems are fairly well preserved and the roots exquisitely so. It has not been possible, however, to work out satisfactorily the structure and course of the leaf traces or leaf bases, and as these have been used chiefly in delimiting species it seems advisable to assign a new specific name to our specimen. The most significant point in the present discussion lies not in the recording of another species of *Mesoxylon* based on trivial or even negative characters but in the presentation of conclusive proof that *Amyelon* is the root of a Cordaitean stem.

The stems attain a diameter of little more than 2 cm. including extra-stelar tissues. The pith in the larger specimens averages about 14 mm. and is typically chambered. The peripheral region consists of large parenchymatous cells about 105 μ in diameter by 60 μ high which are arranged in rather regular vertical rows.

Surrounding the pith are prominent masses of primary wood. These are sufficiently well preserved to state with reasonable certainty that the protoxylem is mesarch (pl. 3, fig. 10). The latter seems to be the only distinctive generic character of *Mesoxylon* segregating it from Cordaites, and in view of the otherwise close similarity between the two the validity of its use as a generic character must be looked upon with some doubt. In a previous paper ('40) I have dealt with the variability in the primary body of the pteridosperms and other groups and have pointed out that the position of the protoxylem must be used with reservation as a taxonomic character.

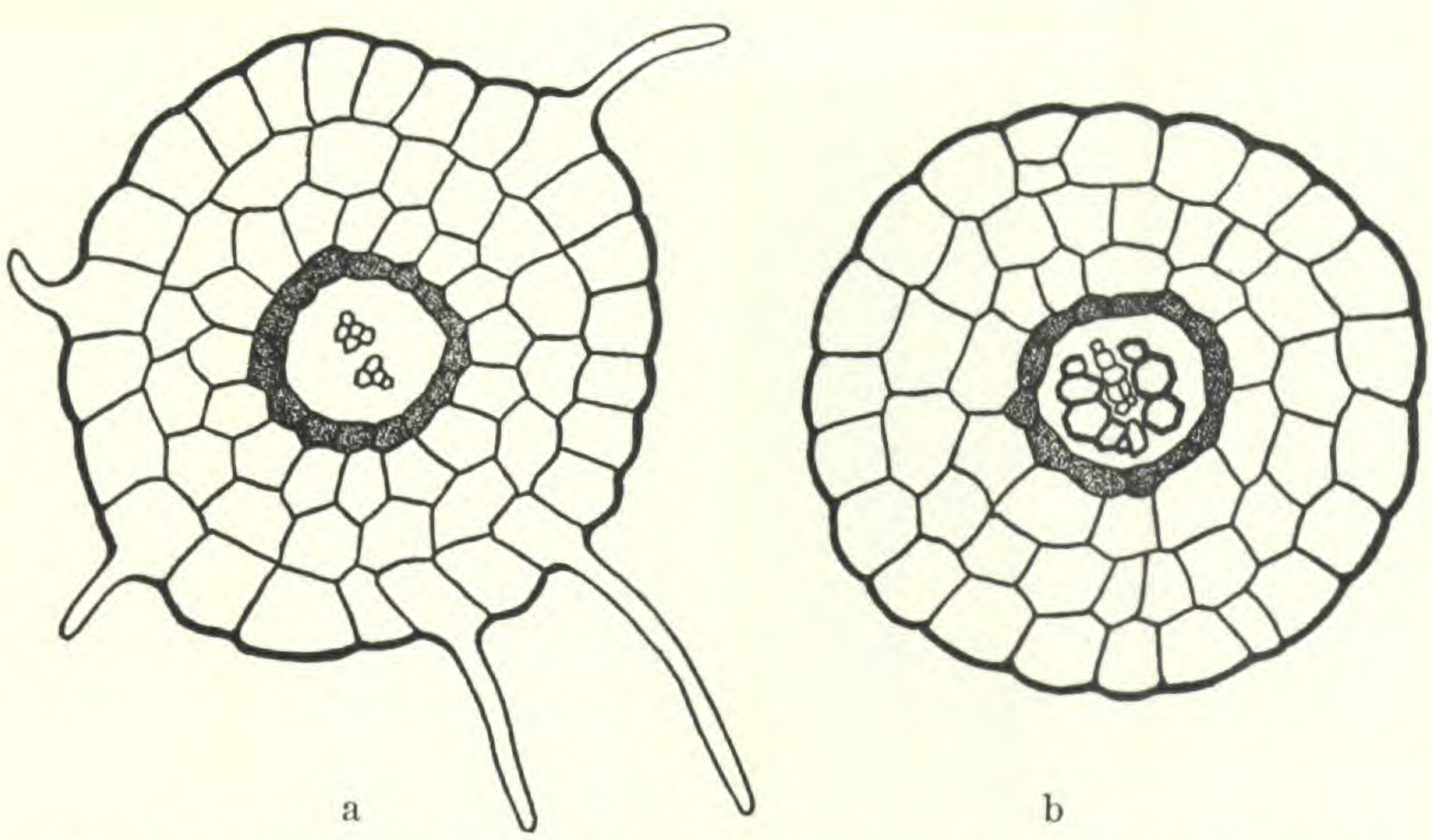
The tracheids of the secondary wood range in cross-section from 15 × 21 μ to 21 × 30 μ, the tangential dimensions being somewhat greater in most cells. As is usual in Cordaitean stems, there is a broad pitting transition zone bordering the pith, the innermost tracheids being spirally thickened. These are followed through a radial distance of about 10 cells by scalariform, reticulate, and pitted cells. The latter are not well preserved, and it is not possible to determine the number of rows of pits per cell. The rays are uniseriate and low, ranging from 1 to 3 cells high (pl. 4, fig. 17) with an occasional ray 4 or 5 cells high.

Roots.—

Well-preserved roots belonging to the form genus *Amyelon* and associated with Cordaitean stem remains have long been known from the Carboniferous of Europe and have more recently been reported in coal-balls from Iowa (Wilson and Johnston, '40). The specimens in our collections from the Pyramid Mine consist of minute rootlets bearing well-preserved hairs up to larger roots 3 mm. in diameter.

There is some question as to the identity of the smallest rootlets, but their association with the older typical specimens of *Amyelon* strongly suggests that they belong to that genus.

In the youngest roots (text-fig. 1*a*) the diarch primary xylem consisting of only 8 or 10 cells, may be observed in the center. All of the roots, young or old, studied thus far are diarch, and the development of the metaxylem is, of course, entirely centripetal. The phloem is not preserved but immediately outside the position it ap-



Text-fig. 1. Rootlets, probably of *Mesoxylon*. In *a* there may be observed the large epidermal cells with root hairs, two layers of cortical cells, the dark endodermis and the diarch primary xylem. In *b* a few secondary xylem cells are present. WCB31F.T5. × 84.

parently occupied is an endodermis the cells of which are filled with a dense brown substance (text-fig. 1, fig. 8). Beyond this is a cortex of larger, thin-walled cells slightly elongated longitudinally. The cells of the epidermis are somewhat larger and thicker-walled.

One of the most interesting features of these rootlets is the beautiful preservation of the root hairs. These may be seen in pl. 3, fig. 8 and at higher magnification in fig. 9. They are clearly typical root hairs, being outgrowths of the epidermis and composed of but a single cell. Most of the young roots show a trace of secondary xylem starting to form (text-fig. 1*b*).

In all the older roots the secondary wood is strongly developed (pl. 4, fig. 16). This is followed by a narrow band of phloem and a cortex of rather large cells many of which appear to be resinous.

The development of periderm started early and all except the smallest roots possess some. The origin of this cork cambial activity was not as deep seated as described by Osborne ('09) for the English specimens, since an appreciable thickness of cortex remains in the older roots. As far as this feature is concerned, the roots described here seem to be intermediate between the English ones and those described by Renault ('79) from France.

The question of the natural affinities of the roots may now be considered. In 1879 Renault noted their association with Cordaitean stems and wrote:

> "Au milieu des mêmes fragments silicifiés que renferment les rameaux et les feuilles de Cordaitales on trouve souvent des débris de racines, dont la structure offre une analogie suffisamment grande avec celle des tiges de ces plantes, pour qu'on puisse les regarder comme ayant appartenu à ces dernieres." [p. 294].

The apparent although unproven significance of this association seems to have been accepted by most paleobotanists, although nearly half a century later Scott ('23) wrote with reference to *Amyelon* that, "they agree so well in histological structure with the stem, that there is no reason to doubt the correctness of Renault's conclusions, that they belonged to the same plants, though I am not aware that roots showing structure have yet been found in actual connection with the stem." [p. 286].

One of our *Mesoxylon* specimens has been found with *Amyelon* roots in actual organic connection, and figs. 13–14 of pl. 4 represent three successive ground sections through part of the stem. In the upper right of fig. 13 a noticeable bulge appears in the periphery; in the next section (fig. 14) the departing adventitious root is very prominent while in the next (fig. 15) it is almost clear of the stem. Fortunately the root was preserved in such a position that immediately after departing from the stem it lay parallel to the latter. Thus, fig. 15 shows the outer part of the root in transverse section and in the next section (fig. 16) the root appears quite separate from the stem and in perfect transverse section. At the left of fig. 15 another root may be seen departing from the stem.

The American and European specimens of *Amyelon* are all so nearly alike that it can now be certainly asserted that they belong to Cordaitean stems. As is usual with roots, their anatomy is more stereotyped than the other vegetative organs, and there seem to be no known dependable characters that make possible the delimitation of distinct species of *Amyelon.* The chief variations in the roots are size, number of protoxylem poles and relative origin of the periderm with reference to the cortex, and none of these (with the possible exception of the last) is sufficient for specific segregation.

Mesoxylon Nauertianum Andrews, sp. nov.

Diagnosis.—

Stems 2 cm. or more in diameter; pith large and chambered; peripheral cells arranged in vertical rows; protoxylem mesarch; secondary xylem tracheids averaging 18 × 25 μ in cross-section, pitting transition broad, rays uniseriate and mostly 1–3 cells high; roots in organic connection with the stem of the *Amyelon* type.

The species is named in recognition of Mr. N. H. Nauert whose willing assistance in the field and ability as a technician has greatly facilitated my coal-ball studies.

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Explanation of Plate

PLATE 1

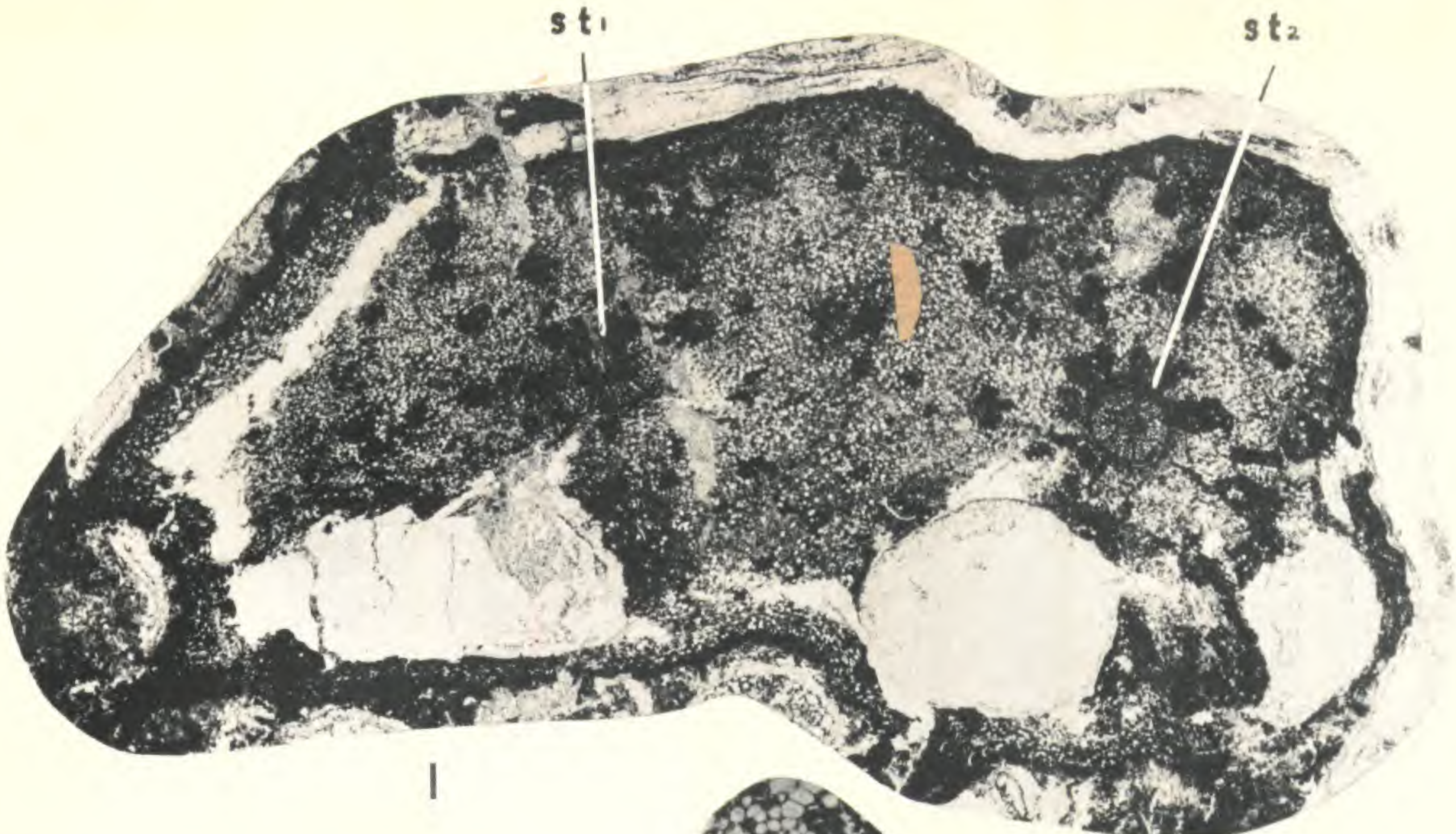
Scleropteris illinoiensis

Fig. 1. Transverse section through the stem showing dichotomy of the stele, *st.* WCB90B.B11, × 4.5.

Fig. 2. Transverse section through the stem; *sc*, sclerotic nests; *st*, stele. WCB90C.T15, × 5.5

Fig. 3. Transverse section through the stele; *mp*, mixed pith; x_2, secondary xylem; *r*, departing root. WCB90C.T2, × 20.

Fig. 4. Longitudinal section through the outer cortex showing bases of emergences. WCB90B.S22, × 17.



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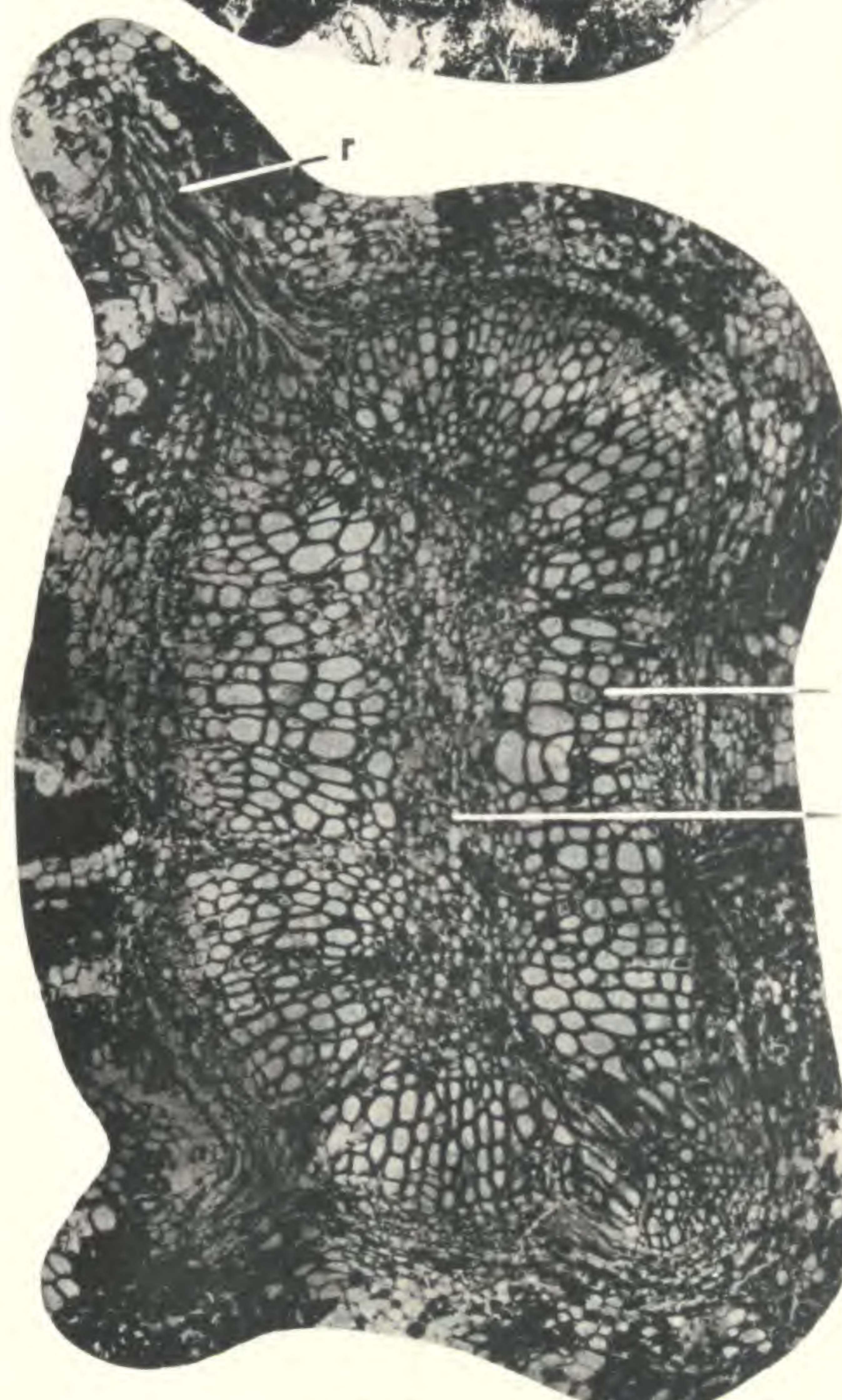

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ANDREWS—AMERICAN CARBONIFEROUS FLORAS. I

Explanation of Plate

PLATE 2

Scleropteris illinoiensis

Fig. 5. Longitudinal section showing branching of stem: *st*, stele; *sc*, sclerotic nests. WCB90B.S35, × 4.

Fig. 6. Longitudinal section through cortex showing an emergence and sclerotic nests. WCB90B.S27, × 8.

Fig. 7. Radial longitudinal section through stele: *px*, protoxylem (?). WCB90B.S22, × 150.

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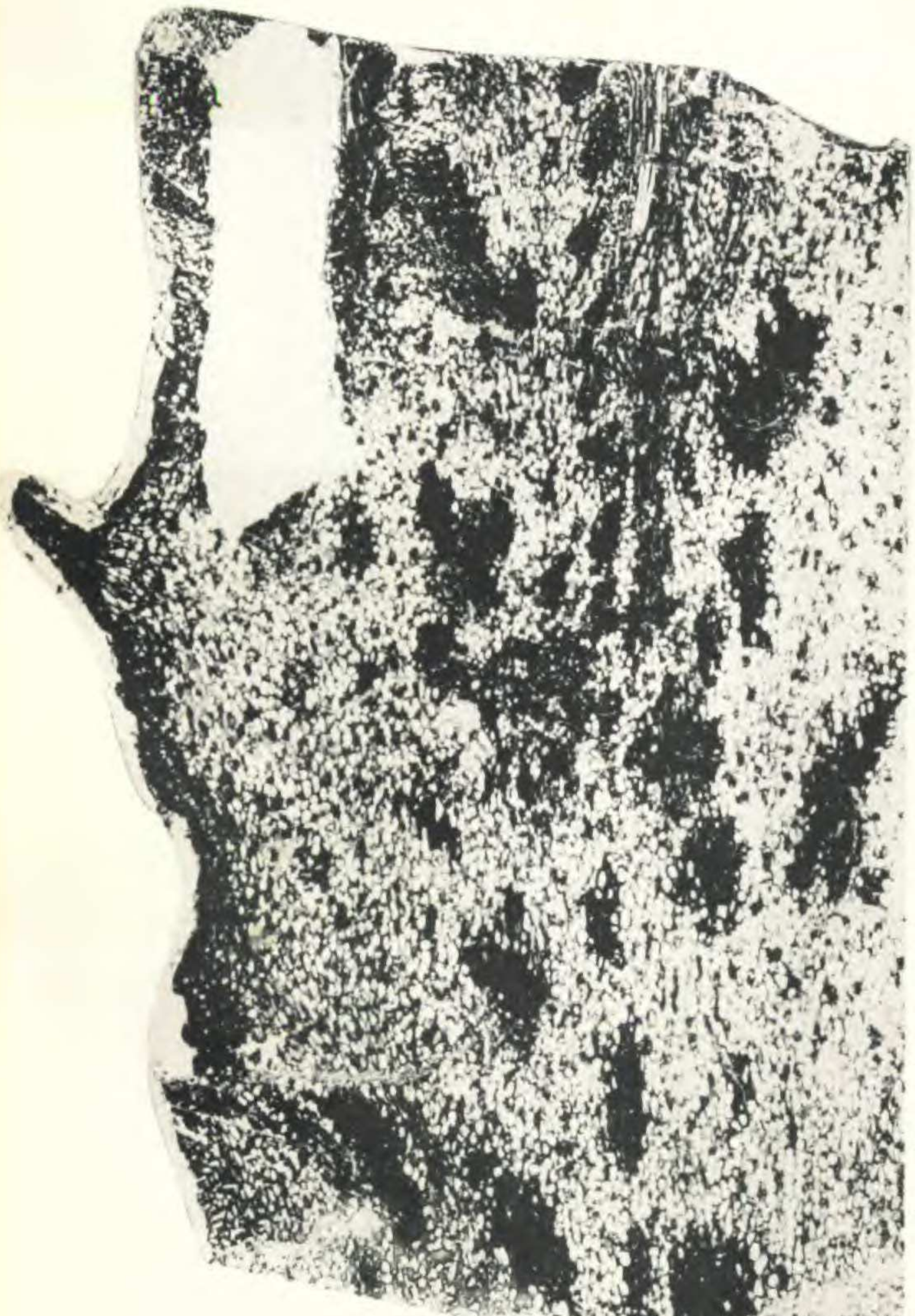

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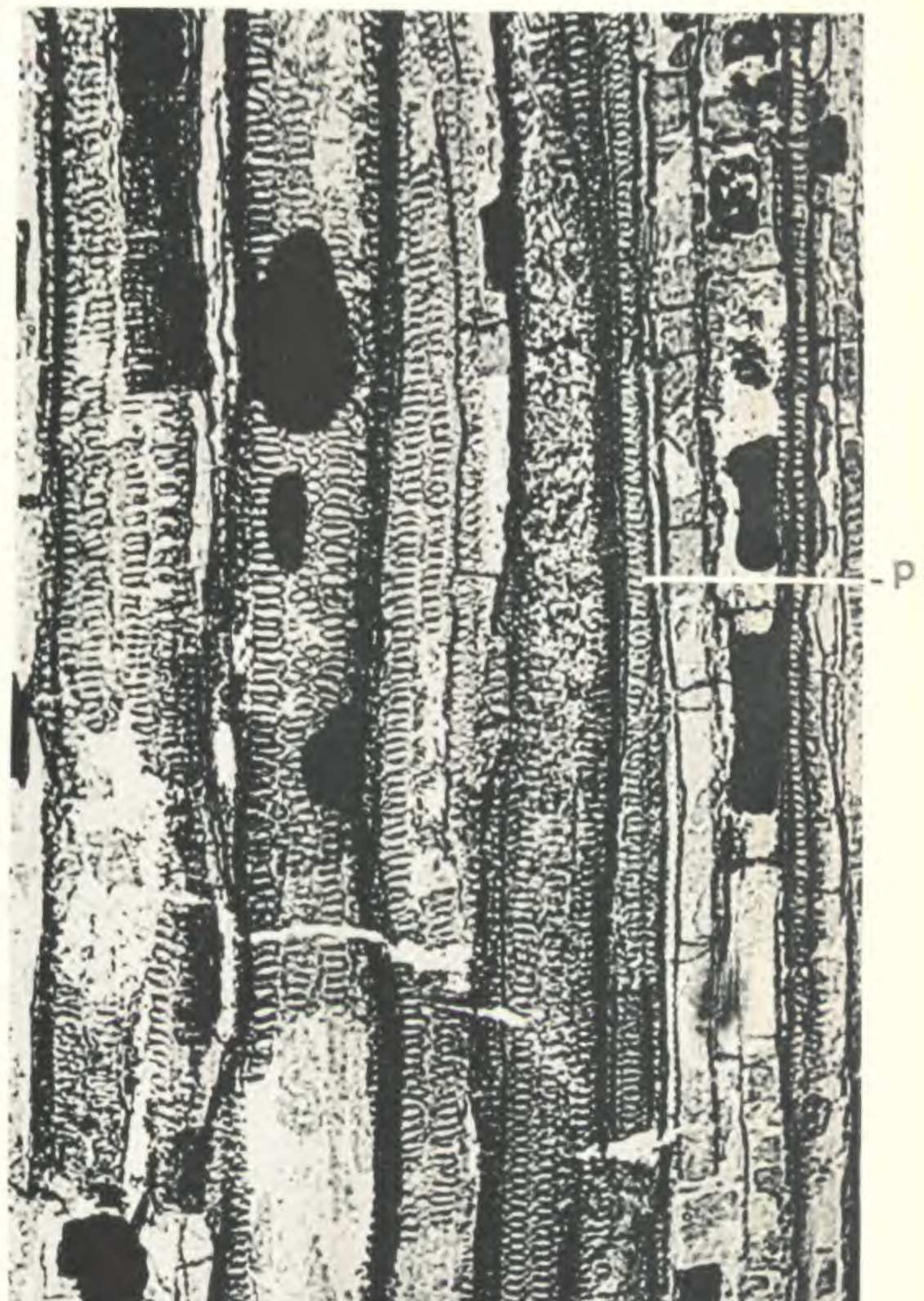

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ANDREWS—AMERICAN CARBONIFEROUS FLORAS. I

Explanation of Plate

PLATE 3

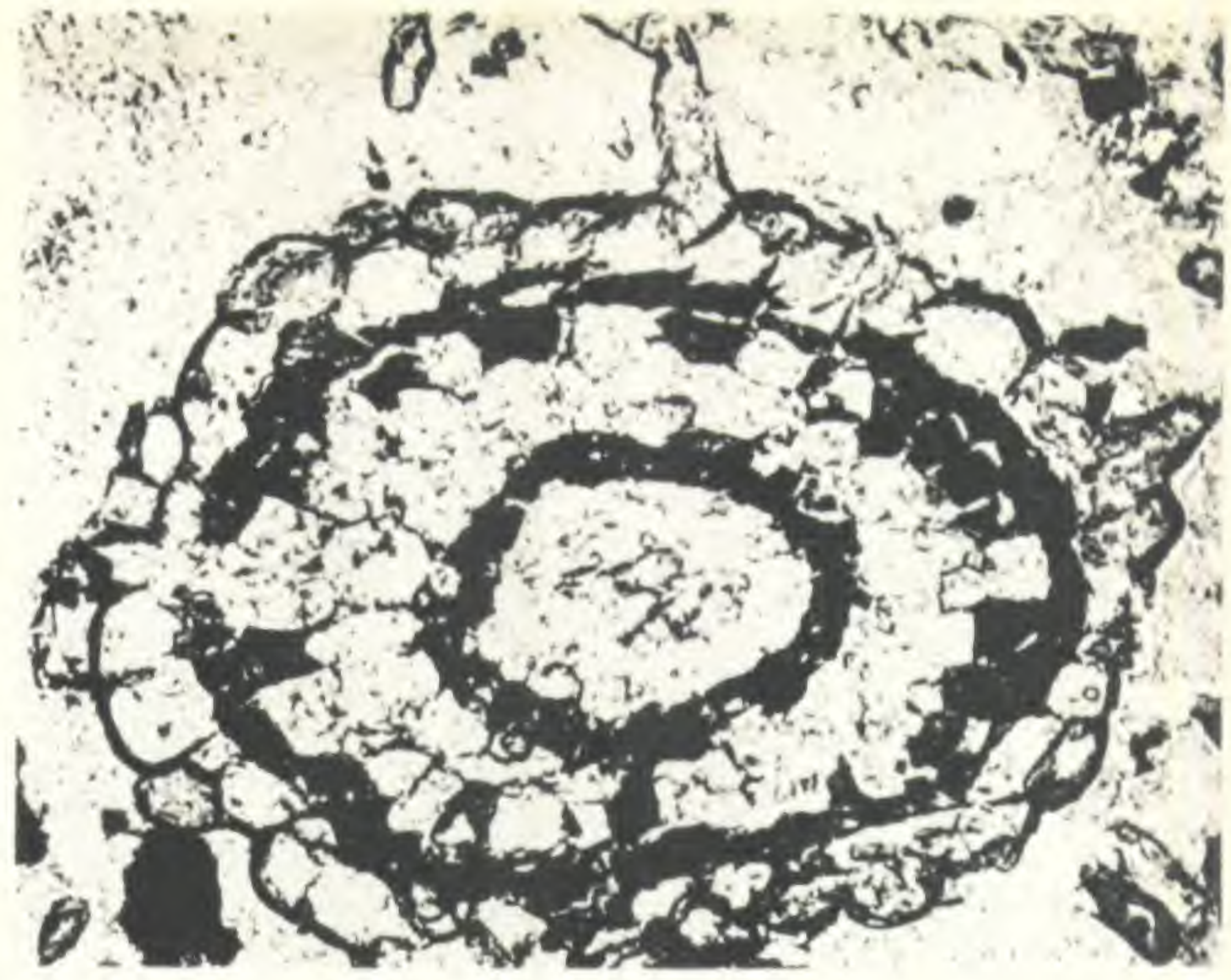
Fig. 8. Rootlet, probably belonging to *Mesoxylon*, bearing root hairs. WCB31F.T4, × 93.

Fig. 9. Portion of another rootlet shown at a higher magnification. WCB31F.T4, × 260.

Fig. 10. *Mesoxylon Nauertianum*. Portion of the stem showing centripetal development of the primary xylem: *p*, pith, *pr*, protoxylem, *m*, centripetal metaxylem, x_2, secondary xylem. WCB53B–B.S8, × 80.

Fig. 11. *Scleropteris illinoiensis*. Tangential section through the central portion of the stem; *r, roots*. WCB90C.T9, × 20.

Fig. 12. *Scleropteris illinoiensis*. Tangential section through the secondary xylem showing tracheids and rays. WCB90B.S32, × 70.



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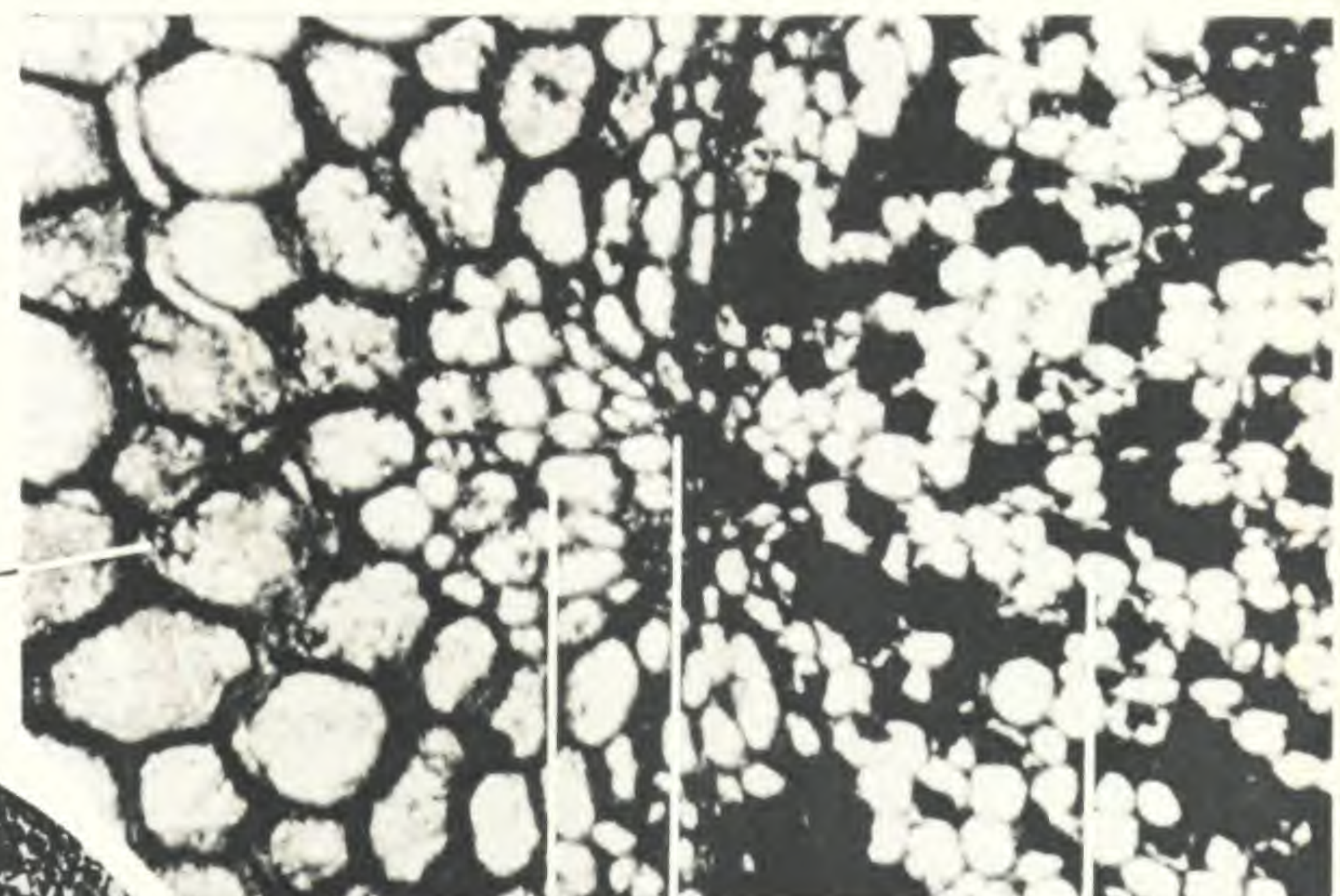

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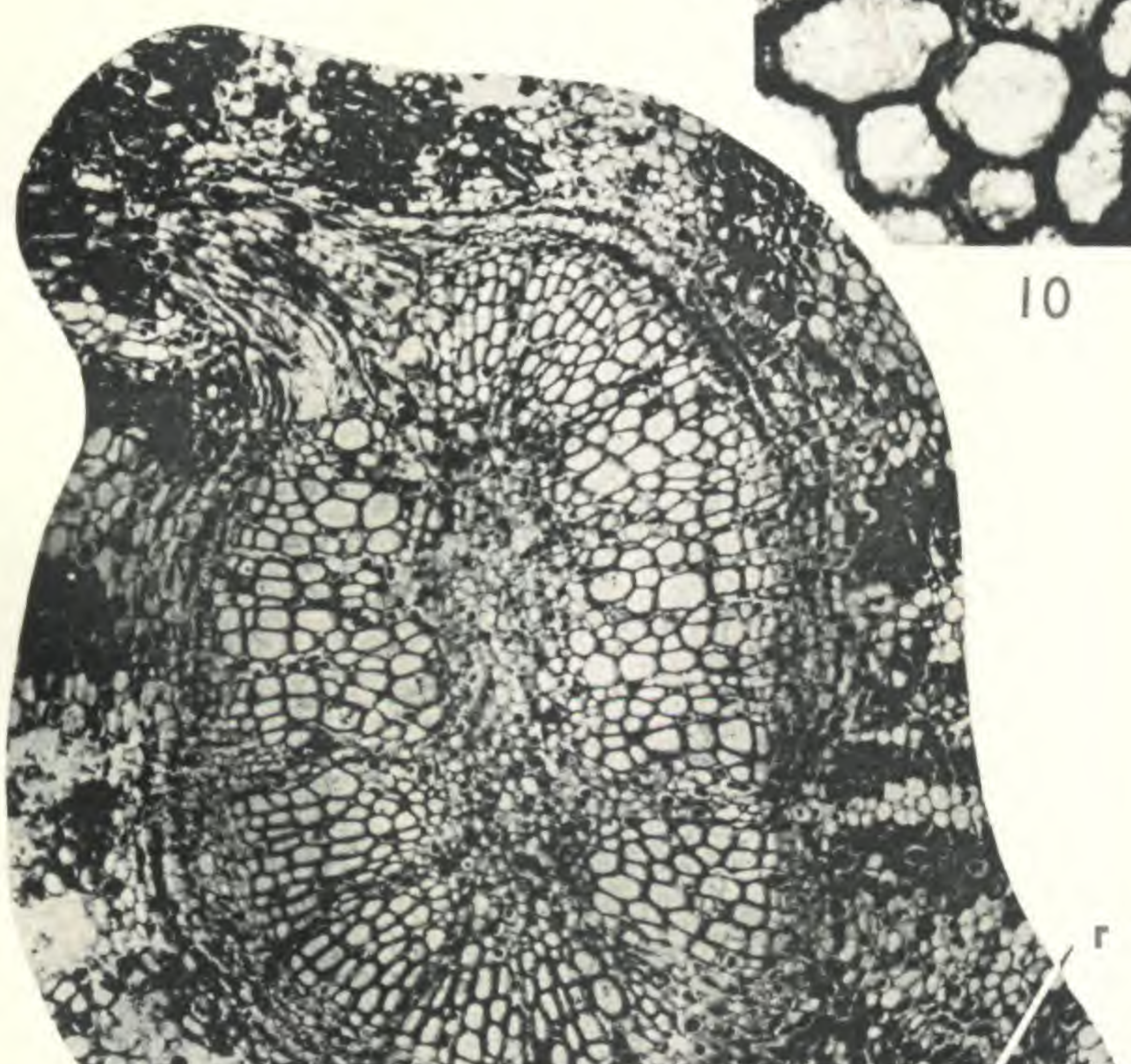

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ANDREWS—AMERICAN CARBONIFEROUS FLORAS. I

Explanation of Plate

PLATE 4

Mesoxylon Nauertianum

Figs. 13–15. Stages in the departure of a root from the stem: fig. 13, WCB92A.1; fig. 14, WCB92A.2; fig. 15, WCB92A.3. All figures × 5.

Fig. 16. Same root as shown in preceding figures after departure from the stem; x_2, secondary xylem; *ph*, phloem; *c*, cortex; *pd*, periderm. WCB92A.4, × 20.

Fig. 17. Tangential section through the secondary wood of the stem. × 110.